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First record of a clupeomorph fish in the Neuquén Group (Portezuelo Formation), Upper Cretaceous of Patagonia, Argentina

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ABSTRACT

A new genus and species of clupeomorph fish, *Leufuichthys minimus*, is described from the fluvial deposits of the Portezuelo Formation, Upper Cretaceous (Turonian–Coniacian) of the Neuquén Group, Patagonia, Argentina. It is a small-sized fish with an estimated body length up to 46 mm. Among other characters, the new species shows the following: abdominal scutes; abdomen moderately convex; anal fin elongate-based; three uroneurals; two epurals; caudal fin bearing very elongate rays; and cycloid scales. *Leufuichthys minimus* gen. et sp. nov. shows a greater similarity with *Kwangoclupea dartevellei*, a clupeomorph described from a marine Cenomanian deposit of the Democratic Republic of Congo (Africa), mainly due to the presence of an elongate-based anal fin, bearing more than 20 fin-rays, differing from it by the presence of a not hypertrophied abdomen. As far as known, *L. minimus* gen. et sp. nov. is the first clupeomorph described in the Upper Cretaceous of Patagonia and represents one fortuitous preservation of an articulated fish in fluvial deposits.

1. Introduction

Clupeomorpha is a diverse, widespread group of fishes containing about 364 living and more than 150 fossil species. The oldest known members are from Lower Cretaceous deposits (Grande, 1985; Murray et al., 2005; Nelson, 2006). The first to diagnose this clade was Grande (1985), based on the following characters: abdominal scutes at the ventral midline; otophysic connection that penetrates the exoccipital forming ossified bullae in prootic and also in the pterotic; supratemporal commissural sensory canal penetrates parietals and supraoccipital; second hypural fused with first ural centrum, and an autogenous first hypural; well-defined preepiotic fossa; and dorsal scutes primitively present. The phylogenetic relationships of the Clupeomorpha have been reviewed by Lecointre and Nelson (1996) and this taxon was proposed as sister-group of Ostariophysi, based on four synapomorphies (i.e., fusion of second hypural and first ural centrum, fusion of extrascapulars and parietals, fusion of haemal spines on centra anterior to second preural centrum, and the presence of a pleurostyle). Arratia (1997, 1999) named the group recognized by Lecointre and Nelson (1996) as Ostarioclupeomorpha pointing out as diagnostic features the primitively ankylosis or fusion between the mesial extrascapular and parietal alone or parietal and supraoccipital, autopalatine ossifying early in ontogeny, and the bases of hypurals one and two not joined by cartilage in any growth stage. Unfortunately, some of those characters are difficult to assess in the majority of clupeomorph fossils.

Since 2000, a large quantity of specimens was collected at the Futalognko Paleontological site in the north coast of Barreales Lake, at the Neuquén Province belonging to the Portezuelo Formation of the Neuquén Group, Upper Cretaceous of Patagonia, Argentina. This site can be considered one of the most important continental Cretaceous Lagerstätten known (Calvo et al., 2007), and although it has been known for a few years, its diversity and quantity of fossils already rival that of other important deposits such as the Santana Formation which is known for several decades (Maisey, 1991; Kellner and Campos, 1999; Fara et al., 2005). Among the fossils that have been collected at the Futalognko site are angiosperm and gymnosperm leaves (Passalia et al., 2008), turtles (fragmentary material), crocodylomorphs (teeth and osteoderms) (Poblete and Calvo, 2005), the giant sauropod *Futalognkosaurus dukei* and remains of two other large titanosaurid sauropod dinosaurs (Calvo et al., 2007), theropods such as *Unenlagia comahuensis* and *Megaraptor namunhuaiquii* (Calvo et al., 2004a,b), one isolated femur of an ornithopod (Porfiri and Calvo, 2002), fragmentary elongatoolithid

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eggshells (Simón et al., 2006), and isolated pterosaur bones, including one very large ulna (Kellner et al., 2007) that shows features observed in the Azhdarchidae (Kellner, 2004; Wang et al., 2009).

Associated with the predominantly reptilian elements, Gallo et al. (2003) briefly noticed the first occurrence of a teleostean fish in the Futalognko Paleontological site, represented only by MUCPv 346. In this site, two other fishes have been collected. One of them is represented by a slab bearing impression of some articulated ganoid scales (Fig. 1), lacking peg and socket articulation (probably from the caudal portion of the body) and an isolated, small, slender, and quadrangular ganoid scale, likely from the anterior portion of the body; it is totally covered by ganoine, and shows a well-preserved peg and an elongate anterior process. The comparisons with similar material (e.g. Brito and Gallo, 2003; Gallo and Brito, 2004; Gallo, 2005; López-Arbarello and Codorniú, 2007) suggest belonging to the Semionotidae. The other taxon is based on an incomplete specimen (MUCPv 599) that exhibits large but narrow vertebrae with a large space among the centra; some large cranial bones are also preserved. The uninformative condition of the material did not allow its taxonomical assignment.

Leufuichthys minimus gen. et sp. nov. is the first record of fishes in the Portezuelo Formation (Neuquén Group) so far and represents a fortuitous occurrence of an articulated specimen in a meandering river. Arratia and Cione (1996) furnished a comprehensive overview of the fossil fishes from southern South America, and according to them, although numerous Upper Cretaceous localities are known, Cretaceous teleosts from there are poorly known. Cione and Lafitte (1980) described a very ancient siluriform in association with a lungfish in the Coli Toro Formation, Upper Cretaceous (Maastrichtian) of Argentina. Cione (1987) studied the fish fauna from the Los Alamitos Formation, Upper Cretaceous (Campanian–Maastrichtian) of Patagonia, regarded to represent a lacustrine paleoenvironment, but with predominance of brackish water. The assemblage is composed by batoids, holosteans, siluriforms, perciforms, and dipnoans. Yet, in the Cretaceous of Argentina, Bocchino (1977) studied the paleofauna of the Agrio Formation from the Lower Cretaceous of Neuquén, pointing out occurrences of pycnodonts and ammonites. The author interpreted the paleoenvironment as marine, neritic, free water, hot and temperate, under the continental shelf. More recently, Apesteguía et al. (2007) accomplished a great review of the Cretaceous Argentinean ceratodontiform records and López-Arbarello and Codorniú (2007) revised the semionotids from the Lagarcito Formation (Lower Cretaceous) originally described by Bocchino (1973, 1974).

In this paper, we describe in detail *L. minimus* gen. et sp. nov. Based on limited information available, this specimen is attributed to the Clupeomorpha on the basis of the presence of abdominal scutes. The main interest in describing this taxon is due to be the first record of a fish in the Portezuelo Formation so far. We also discuss the affinities of the new taxon with some clupeomorphs from the Upper Cretaceous of South America and Africa, as well as with those from the Lower Cretaceous and Tertiary of Argentina. Additionally, we compared *Leufuichthys* with the clupeomorphs from the Lower Cretaceous of Brazil.

1.1. Geological setting

The sedimentary rocks present at the Futalognko site consist mainly of greyish sandstones intercalated with red siltstones of the Portezuelo Formation of the Rio Neuquén Subgroup, Neuquén Group. Based on stratigraphic data, an Upper Cretaceous (Turonian–Coniacian) age is attributed to this unit (Leanza and Hugo, 2001). Three facies are recognized for the upper part of the Portezuelo Formation as follows: sandy channels with mixed-loaded fluvial system, fluvial system of low to moderate sinuosity with predominance of lenticular channels, and architectural elements (*sensu* Miall, 1996) like lateral accretion and overbank facies on the floodplain (Sánchez et al., 2005). The highest part of the unity, where the fish material described here was found, corresponds to a flooding area with well-established bodies of water. Over this sequence a highly sinuous meandering fluvial system was installed. A well-differentiated fluvial system is represented in those units that changes from an intermediate to a high sinuosity system (Sánchez et al., 2005).

1.2. Paleoecology

The fish specimens herein studied were found in a facies with fluvial influence showing meander scars, abandoned channels and crevasse splays. The fishes were preserved in these abandoned channels (or abandoned meanders) and covered by

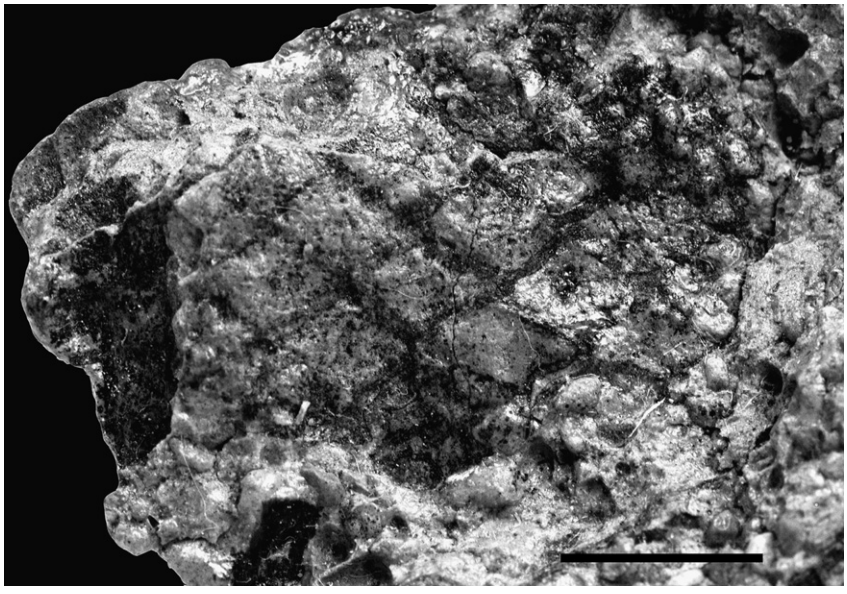

Fig. 1. Impression of some articulated ganoid scales preserved together with the counterpart of MUCPv 348. Anterior is to the left. Scale bar represents 4 mm.

fine-grained sediments. The preservation of fossils within this paleoenvironmental conditions are very unusual, being rarely described in the literature (e.g. Mancuso, 2003; Murray et al., 2005). Generally, fish remains are well-preserved in marine and lacustrine sequences, and appear mainly fragmentary and disarticulated in fluvial deposits. Usually, well-preserved skeletons correspond to mass or seasonal-death assemblages (Grande, 1984, 1988; Smith et al., 1988; Wilson, 1993, 1996) what apparently was not the case here.

2. Material and methods

The material studied herein is preserved in grayish sandstone from the Portezuelo Formation of the Rio Neuquén Subgroup, Neuquén Group. They were collected at the Futalognko Paleontological site, located about 95 km northwest of Neuquén city, at the margins of the Los Barreales lake, Neuquén Province, Patagonia, Argentina. Due to the complete ossification of the bones observed in all skeletons, it is assumed that the specimens represent adult individuals.

The material belongs to the paleontological collection of the Universidad Nacional del Comahue and is designed with the abbreviation MUCPv plus the register number.

All specimens were prepared mechanically with steel needles of different sizes. Ethyl acetate was dropped on the surface of the fossils to enhance skeletal structures. The drawings were made using a camera lucida attached to Nikon SMZ 800 stereomicroscope, as well as photographic magnifications.

Extant clupeomorph fishes were used as comparative specimens, all belonging to the Ichthyological Collection of the Instituto de Biologia of the Universidade do Estado do Rio de Janeiro, which is referred in this paper to the abbreviations AO.UERJ and D.UERJ, followed by the register number. Clupeids are represented by: *Brevoortia* cf. *aurea*, AO.UERJ 112, Itaipu, RJ (dry skeleton; three specimens); *Harengula clupeola*, AO.UERJ 35, 99, no locality data available (dry skeleton; two specimens), D.UERJ 151, Lagoa de Itaipu, RJ (one cleared and stained specimen); *Opisthonema oglinum*, AO.UERJ 126, Rio de Janeiro (dry skeleton; one specimen), D.UERJ 126, Rio de Janeiro (one cleared and stained specimen); *Sardinella brasiliensis*, D.UERJ 79, Baía de Guanabara (one cleared and stained specimen), D.UERJ 176, no locality data available (one cleared and stained specimen). Pristigasterids are represented by *Pellona narroweri*, D.UERJ 175, no locality data available (one cleared and stained specimen). Engraulids are represented by *Anchoa lyolepis*, D.UERJ 125, Rio de Janeiro (one cleared and stained specimen).

Comparative Brazilian fossil clupeomorphs belonging to the paleontological collections of the Departamento Nacional de Produção Mineral (DGM), Museu Nacional of the Universidade Federal do Rio de Janeiro (MN), and Universidade do Estado do Rio de Janeiro (Pz.UERJ) were examined. The taxa are the following: *Codoichthys carnavalii*, DGM 435-P, DGM 436-P, DGM 966-P, from the Upper Aptian of the Grajaú Basin; *Ellimma branneri*, Pz.UERJ 77, Pz.UERJ 95, from the Aptian of the Sergipe-Alagoas Basin; *Ellimma cruzae*, Pz.UERJ 34 to Pz.UERJ 36, Pz.UERJ 502 to Pz.UERJ 507, from the Aptian-Albian of the Pernambuco Basin; *Ellimmichthys longicostatus*, MN 4424-V, MN 4428-V, MN 4433-V, MN 4434-V, MN 4438-V, MN 4439-V, MN 4443-V, MN 4444-V, from the Neocomian of the Recôncavo Basin; *Santanaclupea silvasantosi*, DGM 515-P, DGM 1338-P, from the Albian of the Araripe Basin; *Scutatuspinosus itapagipensis*, DGM 1164-P to DGM 1176-P, DGM 1207-P to DGM 1264-P, from the Neocomian of the Recôncavo Basin.

2.1. Anatomical abbreviations

We use (r) and (l) after abbreviations of anatomical structures to indicate right and left side, respectively. **AF**, anal fin; **AO**, antorbital; **ASPH**, autosphenotic; **BAS**, basisphenoid; **BRR**, branchiostegal rays; **CdR**, caudal fin-rays; **CL**, cleithrum; **D**, dentary; **dpr**, dorsal pre-current rays; **ECT**, ectopterygoid; **EP**, epural; **EPN**, epineural; **EPO**, epioccipital; **EPP**, epipleural; **EXT**, lateral extrascapular; **FR**, frontal; **H**, hypural; **HM**, hyomandibula; **hs**, haemal spine; **IO**, infraorbital; **IOP**, interopercle; **LA**, lacrimal; **LET**, lateral ethmoid; **ll.c.**, lateral line canal; **md.c.**, mandibular sensory canal; **MX**, maxilla; **NA**, nasal; **ns**, neural spine; **OP**, opercle; **PA**, parietal; **PAS**, parasphenoid; **PB**, pelvic bone; **PCL**, postcleithrum; **PH**, parhypural; **PMX**, premaxilla; **POP**, preopercle; **PRO**, prootic; **PT**, posttemporal; **p.fo.**, posttemporal fossa; **pPTG**, proximal pterygiophore; **PTO**, pterotic; **PTS**, pterosphenoid; **PU**, preural centrum; **PtR**, pectoral fin-rays; **PvR**, pelvic fin-rays; **RAD**, radial; **rb**, rib; **SCL**, supracleithrum; **so.c.**, supraorbital sensory canal; **SOP**, subopercle; **SORB**, supraorbital; **U**, ural centrum; **UN**, uroneural; **vc**, vertebral centrum; **vs**, ventral scute.

2.2. Institutional abbreviations

AO.UERJ and D.UERJ, Instituto de Biologia of the Universidade do Estado do Rio de Janeiro; MUPCPv, Centro Paleontológico Lago Barreales, Universidad Nacional del Comahue.

3. Systematic Paleontology

Teleostei Müller, 1844

Clupeomorpha Greenwood et al., 1966 *incertae sedis*

Leufuichthys gen. nov.

Type and only known species – *L. minimus* sp. nov.

Etymology – The generic name is formed by "Leufu", a Mapuchi Indian word for river or estuary, and "ichthys", the Greek word for fish.

Diagnosis – Small-sized fish (estimated body length up to 46 mm) exhibiting the following combination of features: fairly deep body ventrally armored of acute triangular scutes; dermal skull bones smooth; small oval posttemporal fossa; small orbit fitting about five times in the head length; small and oblong supraorbital bone; premaxilla and dentary untoothed; fairly deep lower jaw; narrow opercle, about twice higher than long; vertebral centra well-ossified and smooth bearing well-developed haemal and neural arches; elongate and arched pleural ribs lying on short parapophysis; intermuscular bones present in the caudal region; anal fin elongate-based, with about 25 rays; 18 caudal vertebrae; haemal spines anterior to the second preural centrum fused to their respective centra; slender and autogenous parhypural; six hypurals, the first one being the largest of the set; no diastema among the hypurals; two rod-like epurals; three uroneurals, the first one extending forward to the posterior end of the first preural centrum; caudal fin bearing very elongate rays surpassing the anal base length.

Leufuichthys minimus sp. nov.

(Figs. 2–8)

Holotype – MUCPv 371, an incomplete specimen missing most of the cephalic skeleton, preserved in part and counterpart.

Paratypes – MUCPv 344 (part and counterpart), incomplete specimen lacking head; MUCPv 346, incomplete specimen lacking most of skull; MUCPv 347, incomplete specimen bearing scales; MUCPv 348 (part and counterpart), incomplete specimen with skull and part of trunk.

Etymology – The specific Latin epithet "minimus" is in allusion to the reduced size of this taxon.

Diagnosis – As for the genus.

Type locality – Futalognko Paleontological site, located about 95 km northwest of Neuquén city, at the margins of the Los Barreales lake, Neuquén Province, Patagonia, Argentina.

Stratigraphy – Upper Cretaceous (Turonian–Coniacian), Portezuelo Formation, Rio Neuquén Subgroup, Neuquén Group.

4. Descriptive morphology

4.1. General features

Leufuichthys minimus gen. et sp. nov. (Figs. 2–8) is a very small and fairly compressed fish, deepened in the abdominal region but not forming a prominent abdomen. The body length was estimated of about 46 mm and the maximum body depth, measured from the dorsalmost to the ventralmost points of the body contour, reaches 16 mm. The bones of the dermal skull are smooth. The mouth is large and the orbit is reduced. Dorsal fin is short-based whereas the anal fin is elongate-based. The caudal fin seems to be of the homocercal forked type. There are at least 14 abdominal scutes and cycloid scales. A partial reconstruction of the holotype (MUCPv 371 a, b), preserved in part and counterpart, is illustrated in Fig. 2.

4.2. Skull

Most of skull is lost or poorly preserved in the majority of specimens, being the description based on the specimen MUCPv 348 (part and counterpart). Even so, some bones are reconstructed in Fig. 3D.

Only the lateral ethmoid (Fig. 3) is preserved from the ethmoidal region. Although incomplete, it seems to be a large laminated bone, which extends downwards and reaches the parasphenoid.

The nasal (Fig. 3) is a reduced tubular bone, which contacts the anterior border of the frontal and is tightly associated to the antorbital. The supraorbital sensory canal runs across the bone in the midline, being recognized externally by the presence of, at least, two pores.

The frontal (Fig. 3) is a very elongate bone with a slightly convex profile. Anteriorly, it is more slender expanding posteriorly. It meets the parietal rear through a straight suture and the autosphenotic,

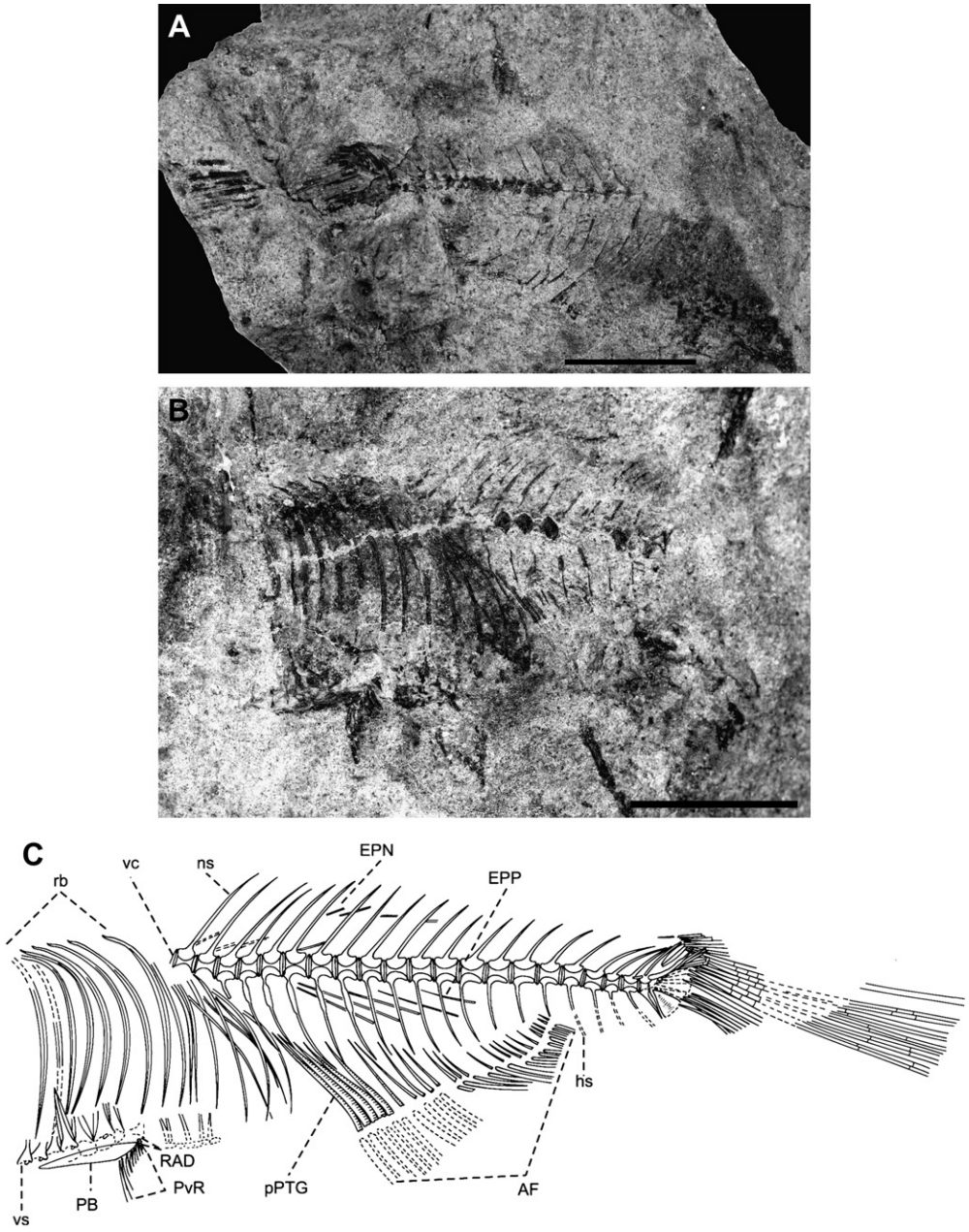

Fig. 2. Holotype of *Leufuichthys minimus* gen. et sp. nov. (MUCPv 371). A, part, in right lateral view; B, counterpart, in left lateral view; C, reconstruction based on part and counterpart and illustrated in left lateral view (dotted lines indicate reconstructions of poorly preserved structures). Scale bars represent 6 mm.

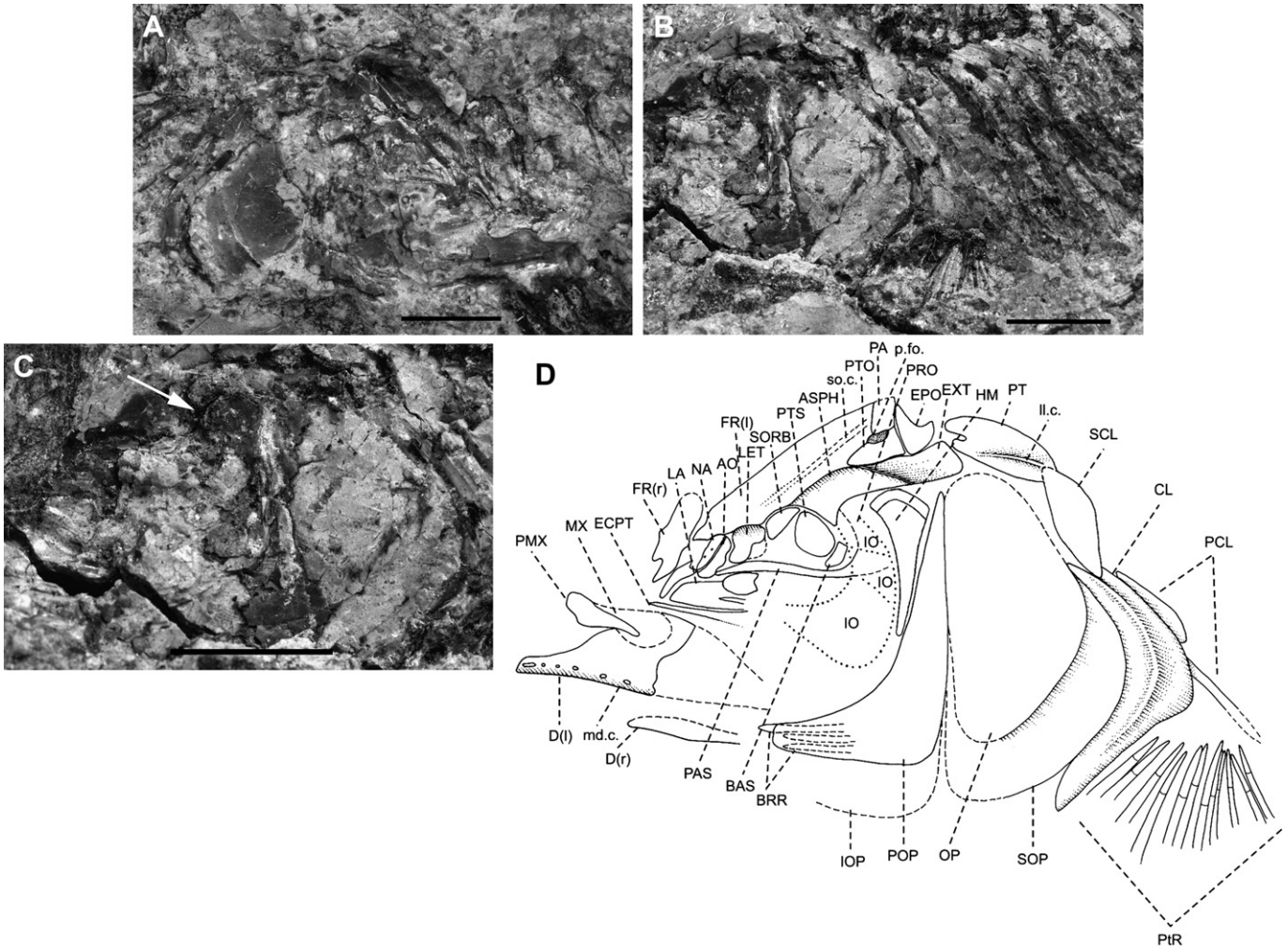

Fig. 3. *Leufuichthys minimus* gen. et sp. nov. (MUCPv 348). A, skull (part, in right lateral view); B, skull and part of the trunk (counterpart, in left lateral view); C, close-up of the hyopalatine and opercular series (counterpart, in left lateral view), showing the well-preserved hyomandibula (arrow); D, interpretative drawing based on part and counterpart and illustrated in left lateral view (dotted lines indicate reconstructions of poorly preserved structures). Scale bars represent 5 mm.

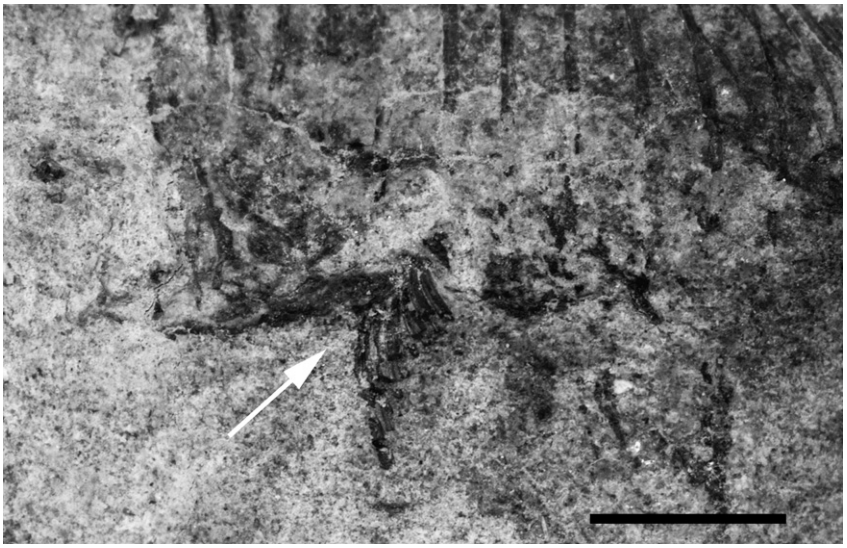

Fig. 4. Detail of the pelvic girdle and fin (arrow) of *Leufuichthys minimus* gen. et sp. nov. as preserved in the holotype (MUCPv 371, counterpart), in left lateral view. Scale bar represents 3 mm.

Fig. 5. Incomplete specimen of *Leufuichthys minimus* gen. et sp. nov. (MUCPv 344, counterpart) showing dorsal fin (arrow), in right lateral view. Scale bar represents 11 mm.

posterolaterally. The supraorbital sensory canal runs in a narrow tube at the lateral portion of the bone. A piece of bone placed near the anterior end of the left frontal was interpreted as part of the right frontal.

The parietal (Fig. 3) is incompletely preserved, but judging by the corresponding topographical space, it appears to be a small quadrangular bone. Due to the poor preservation, it is impossible to verify a contact (or not) between parietals.

The supraoccipital is not preserved, but judging by the space between parietal and epioccipital it was a small bone. The bad preservation of parietal and supraoccipital did not allow to verify the typical canal for the supratemporal commissure.

Only the anterior part of the pterotic is observed (Fig. 3), due to the posterior one being covered by the rectangular lateral extrascapular. It shows a narrow trapezoidal shape and is placed at the dorsolateral border of the otic region; anteriorly it contacts the autosphenotic. Due to the posterior part of the pterotic is hidden by the extrascapular, it was not possible to verify if the recessus lateralis is present or not.

Frontal, parietal, and pterotic delimit a small oval posttemporal fossa (Fig. 3).

The autosphenotic (Fig. 3) is a well-developed wedge-shaped bone. It is placed at the posterodorsal limit of the orbit, being bordered by the pterotic and lateral extrascapular posteriorly and by the frontal medially. The autosphenotic contributes in part to the articular facet for anterior head of hyomandibula. Laterally, the bone produces a short spine-like process slightly directed backwards.

The pterosphenoid (Fig. 3) is a large subrounded bone with an almost straight anterior border. Posteroventrally, it meets the oblique anterior border of the basisphenoid (Fig. 3). From this bone, only a piece of the belophragme is preserved at the posteroventral corner of the orbit near the ascendant process of the parasphenoid. Pterosphenoid, orbitosphenoid (not preserved), and basisphenoid seem to compose a well-ossified interorbital septum.

The epioccipital (Fig. 3) is a large triangular bone, contacting parietal, pterotic, and lateral extrascapular through straight sutures. It possesses a smooth dorsal surface for receiving the dorsal arm of the posttemporal.

The parasphenoid (Fig. 3) is a slender, elongate, and untoothed bone, forming the greatest part of the basicranium. It extends

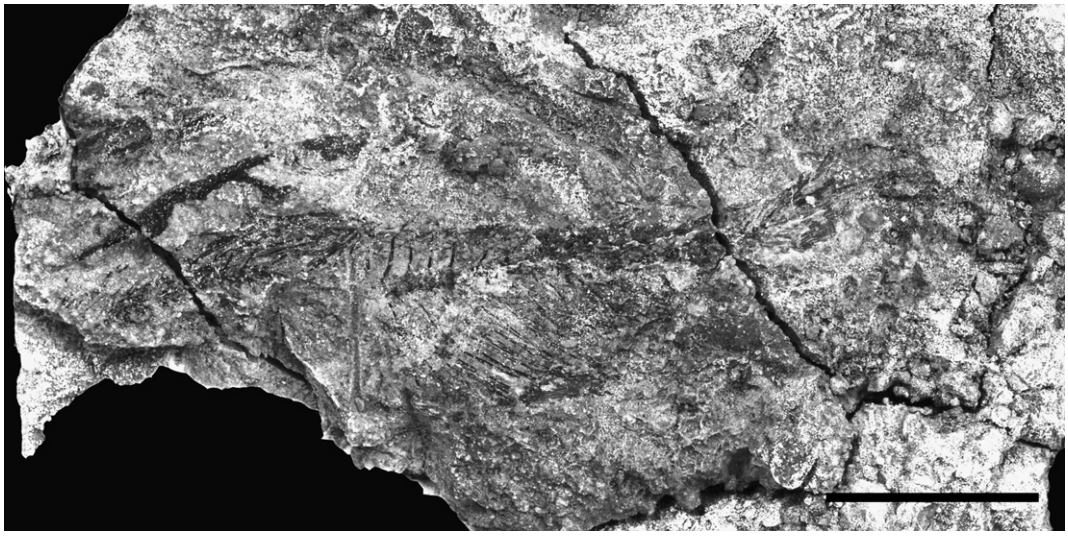

Fig. 6. Incomplete specimen of *Leufuichthys minimus* gen. et sp. nov. (MUCPv 346), showing the moderately convex abdomen, in left lateral view. Scale bar represents 12 mm.

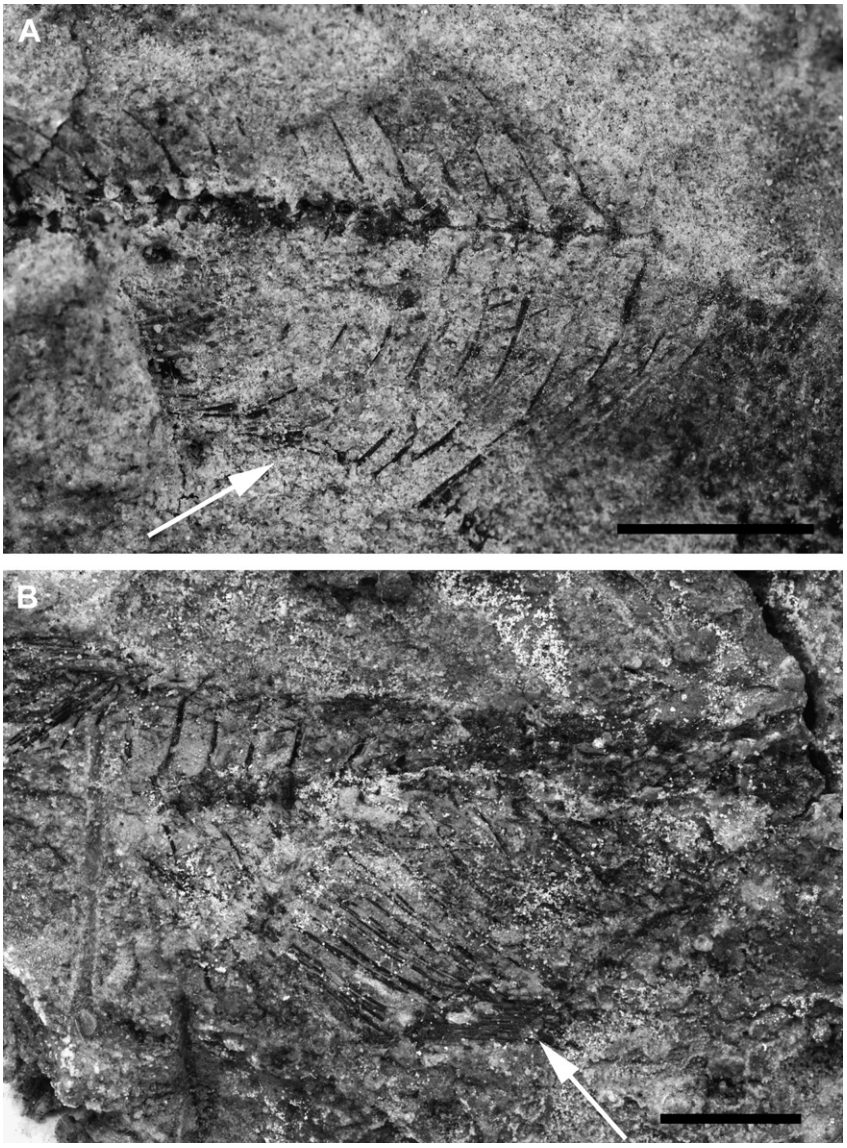

Fig. 7. Detail of the anal fin (arrow) of *Leufuichthys minimus* gen. et sp. nov. A, holotype (MUCPv 371, part, in right lateral view); B, MUCPv 346, in left lateral view. Scale bars represent 4 mm.

forwards surpassing the limit of the lateral ethmoid. A basipterygoid process appears to be lacking. The bone is dorsally keeled and horizontally oriented along almost all of its extent except for the posterior corner of the orbit where the bone inclines obliquely upwards. In this point, located at the level of the autosphenotic spine, the parasphenoid produces a short ascendant process dorsally that meets the prootic bone, which is poorly preserved preventing a detailed description.

4.3. Circumorbital series

This series is described on the basis of the specimen MUCPv 348 (part and counterpart).

A small and oblong supraorbital bone (Fig. 3) is obliquely positioned in relation to the orbit. The bone contacts anteriorly the lateral ethmoid, medially the anterolateral portion of the frontal, and reaches the autosphenotic rear.

The antorbital (Fig. 3) is an elongate bone, which contacts the nasal dorsally. It is placed near the anterior end of the frontal. Apparently, it lacks a passage for the infraorbital sensory canal.

Although the lacrimal (Fig. 3) is incompletely preserved, it seems to be a large rectangular bone. The third infraorbital (Fig. 3) is a very large trapezoidal bone possessing an expanded laminate posterior portion. There are no vestiges of the second infraorbital and the remaining infraorbitals are not well-preserved. Apparently the infraorbital bones do not cover the cheek completely, so that the hyomandibula is exposed.

4.4. Upper jaw

The upper jaw is preserved only in the part of the MUCPv 348.

The premaxilla (Fig. 3) is a subtriangular and relatively elongate bone, its depth being about half of the length. Anterodorsally, the bone possesses a short and rounded ascending process. The oral border seems to be untoothed.

Only faint imprint of the maxilla (Fig. 3) is available and does not allow a detailed description. There is no trace of supramaxilla.

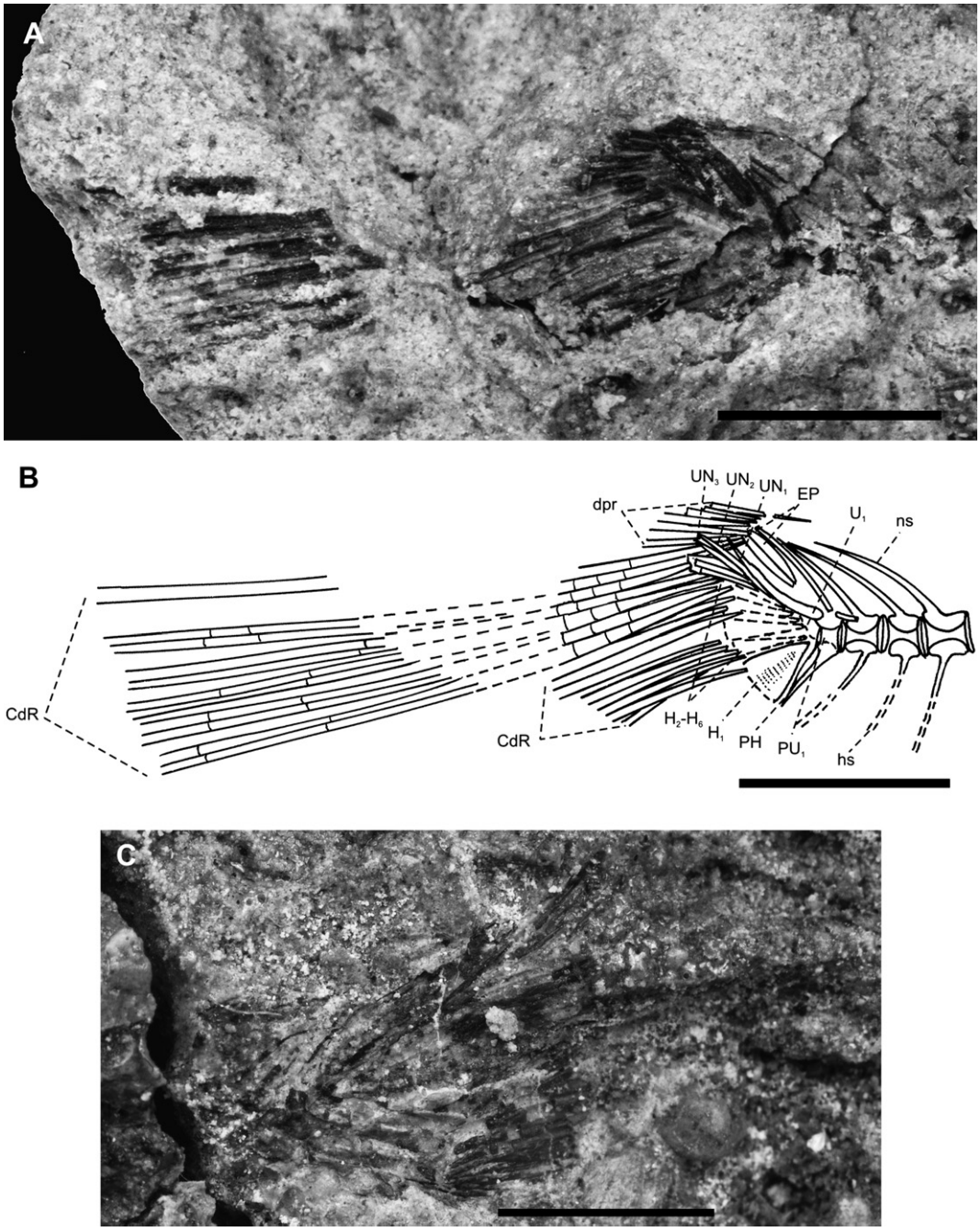

Fig. 8. Caudal skeleton and fin of *Leufuichthys minimus* gen. et sp. nov. A, photograph of the holotype (MUCPv 371), in right lateral view; B, line drawing of A (dotted lines indicate reconstructions of poorly preserved structures); C, photograph of MUCPv 346, in left lateral view. Scale bars represent 5 mm.

4.5. Lower jaw

Although the skull is incompletely preserved in MUCPv 348, the lower jaw seems to possess a pronounced prognathism. Only the dentary and a small fragment of the anguloarticular (Fig. 3) are preserved in the lower jaw. The dentary is relatively deep, being deeper in the rear, as typical of most clupeomorphs. It shows a low symphysis and a high coronoid process. Teeth are lacking. The mandibular sensory canal runs parallel and close to its ventral margin; it is observed externally due to the presence of six pores. The suture with the anguloarticular is sinuous. A piece of bone placed ventrally to the lower jaw was interpreted as a fragment of the right lower jaw. The quadrate-mandibular joint seems to be placed at the level of the mid-point of the orbit.

4.6. Opercular series

This series is described on the basis of the specimen MUCPv 348 (part and counterpart).

The preopercle (Fig. 3) is L-shaped with the lower limb shorter than the upper limb. This latter is vertically oriented and surpasses the level of the opercular process of the hyomandibula (not preserved). An obtuse angle is formed between the limbs. Due to the poor preservation of this bone, the preopercular sensory canal was not observed.

The opercle (Fig. 3) is a large trapezoidal bone, about twice as high as long. It is slightly oblique in relation to the main head axis. Its ventral border is larger than the dorsal one. The bone is devoid of ornamentation.

The subopercle (Fig. 3) is narrow and falcate, and possesses a short anterodorsal process. The interopercle (Fig. 3) is poorly preserved, but it appears to be an elongate triangular bone partially hidden by the ventral border of the preopercle.

4.7. Hyopalatine series

From this series, only the hyomandibula and part of the ectopterygoid are preserved in MUCPv 348 (part and counterpart).

The hyomandibula (Fig. 3) is a narrow bone whose main body apparently possesses a straight orientation in respect to the head axis. It possesses a continuous and fairly oblique articular facet, more elongated posteriorly. The vertical arm is long and thin and seemingly does not produce anterior laminate outgrowth. The opercular process is not preserved.

An elongate and thin piece of bone placed dorso-medially in relation to the lower jaw was interpreted as the anterior portion of the ectopterygoid (Fig. 3).

4.8. Hyoid arch

Three slender pieces of bone preserved under the preopercle are interpreted as branchiostegal rays (Fig. 3).

4.9. Vertebral column, ribs, and intermuscular bones

The abdominal region of the vertebral column is incompletely preserved in all examined specimens, being best seen in the holotype (Fig. 2). Only three vertebral centra and 18 pleural ribs are preserved in this region, but judging by the number of ribs, there were at least more than 10 abdominal centra (one pair of ribs by centra). Thus, the total number of vertebrae is unknown, but it is estimated in 31, from which 18 are caudal, not including the urals. Centra are well-ossified, smooth, and spoon-shaped all along the vertebral column showing a remarkable constriction. They are slightly longer than deep and bear well-developed haemal and neural arches. Anteriormost vertebrae show single (not bifid), long, and straight neural spines, becoming gradually short and inclined backwards. The haemal spines of the first five caudal vertebrae possess a proximal protuberance as a continuation of the haemal arch. The haemal spines decrease progressively backwards (Fig. 2).

Eighteen long pleural ribs (Fig. 2) are preserved almost reaching the ventral margin of the body, some of them contacting the abdominal scutes. They exhibit a marked concavity directed forwards. The eight first ribs are stout and longitudinally keeled, whereas the remnants are more slender and smaller. Only one rib at the end of the abdominal region allows to see its attachment to a short parapophysis (Fig. 2). The preservation impedes to verify if the parapophysis is fused to the centrum, as seen in Clupeiformes.

Epineural intermuscular bones are very scarce, being short and apparently not fused to the base of the neural arches. They extend to the caudal region. Epipleural intermuscular bones are also scarce, but they are elongate, and apparently they are restricted to the caudal region (Fig. 2).

4.10. Pectoral girdle and fin

From the pectoral girdle, posttemporal, supracleithrum, cleithrum, and postcleithra are preserved in MUCPv 348 (part and counterpart).

The posttemporal (Fig. 3) is a large bone with dorsal and ventral limbs almost equal in length, being the dorsal slightly arched. An oblique branch of the sensory canal for the lateral line pierces the posteroventral border of the posttemporal where it contacts the supracleithrum.

The spatulate supracleithrum (Fig. 3) lies oblique and laterally on the upper third of cleithrum. The latter is a stout L-shaped bone (Fig. 3), showing a smooth outer surface. Both limbs are approximately equal in size and the dorsal one shows a reduced dorsal spine-like process. A crest strengthens the midline of the bone producing a relatively expanded outer laminate surface.

There are, at least, two aligned postcleithra (Fig. 3) inclined backwards. The dorsal postcleithrum is a spatulate bone, whereas the ventral one is an elongate rod-like bone.

The pectoral fin (Fig. 3) is best seen in the counterpart of MUCPv 348. It is displaced from its anatomical position and bears at least 12 equal-sized segmented rays.

4.11. Pelvic girdle and fin

The pelvic girdle and fin are badly preserved in MUCPv 371 (Figs. 2 and 4) and MUCPv 348 (counterpart, not figured), but the description is based on mainly the former. The pelvic bone seems to be elongate and triangular in shape. The pelvic fin lies in an abdominal position and bears about eight fin-rays. Two nodular pieces of bone placed medially to the pelvic bone and associated with some fin-rays are interpreted as radials (Figs. 2 and 4).

4.12. Dorsal fin

The dorsal fin is preserved only in MUCPv 344 (counterpart, Fig. 5). It is slightly displaced from its usual anatomical position, but it seems to be sited between the pelvic and anal fins origin. It is short-based and bears at least 10 elongate rays. The pterygiophores are badly preserved, but the first one appears to be the largest of the set.

4.13. Anal fin

The anal fin can be observed in the specimens MUCPv 344 (counterpart, Fig. 5), MUCPv 346 (Figs. 6 and 7), and MUCPv 371 (Figs. 2 and 4), but the description is based on mainly in the latter. It is elongate-based, bearing about 25 fin-rays, the same number of preserved proximal pterygiophores. However, there are only impressions of the ten first rays, which are based mostly on the pterygiophores. All pterygiophores are slender, being the first two very elongate, decreasing in size posteriorly. The first five pterygiophores exhibit a sigmoid profile, whereas the remnants are almost straight. The rays are thin and rod-like structures.

4.14. Caudal skeleton and fin

The caudal fin is incompletely preserved in the specimens MUCPv 344 (counterpart, Fig. 5), MUCPv 346 (Figs. 6 and 7), and MUCPv 371 (Fig. 8), but the description is based mainly on the latter. The fin seems to be forked and the principal rays are very long surpassing the anal base length. It is displaced from its anatomical position, but we recognized a total of 17 principal segmented rays, but it was not possible to define the boundary of the two sets of principal fin-rays. Yet, it is not clear the position of the dorsal and ventral principal segmented and unbranched rays. There are, at least, five dorsal precurrent rays, but ventral ones are not preserved. Two slender pieces of bone inserted between uroneurals and hypurals are interpreted as pieces of rays (Fig. 8).

The endoskeleton (Fig. 8) is damaged not allowing to verify the exact number of the ural centra. Hypurals are not completely

discernible, but faints of six of them are present. The first hypural is better preserved, showing to be the largest of the set. Proximally, it seems to contact the base of the first ural centrum, as it does in second and third hypurals. The second hypural is slender and long almost equal in shape and size to the fourth, fifth, and sixth hypurals, but differing from the third which is slightly larger. A slender parhypural seems to be free from the first preural centrum; it produces a fairly posterior laminate outgrowth. From the second to the fourth preural centra are hour-glass shaped and bear long and thin neural spines curved backwards. The first preural centrum is smaller than the other three and appears to bear a long neural spine. Except for the parhypural, apparently there are no autogenous neural and haemal structures, and the haemal spines placed ahead the second preural centrum are fused to their respective centra. There are two elongate rod-like epurals. There are three uroneurals. The first one is the longest, slightly curved, extending forward to the posterior end of the first preural centrum, being free from it, that is, they do not form a pleurostyle. The second and third uroneurals are shorter, more slender, and rectilinear, being the former the smallest of them.

4.15. Squamation

Scales are preserved only in MUCPv 347 (not figured). They are small and cycloid-type, deeply imbricated, and almost vertically disposed on the body, exhibiting several concentric circuli on surface.

4.16. Abdominal scutes

Abdominal scutes are damaged, but there are 14 scutes in MUCPv 371 (Fig. 2), six of them preserved posterior to the pelvic fin. They seem to be elongate, subtriangular, and smooth, bearing a long ascending arm of about 3 mm long. Anteriorly and posteriorly each scute produces two short ventral processes, which are overlapped. They slightly decrease in size after the pelvic fin.

5. Discussion and Conclusions

To our knowledge, *L. minimus* represents the first Clupeomorpha in the Portezuelo Formation, Upper Cretaceous of Patagonia, Argentina, being an exceptional example of articulated fish material from a fluvial deposit. The occurrence of fishes in other Cretaceous deposits of Argentina is relatively rare and none represents a typical fluvial environment (see Arratia and Cione, 1996).

According to the current classification of Clupeomorpha (e.g. Grande, 1985; Maisey, 1993; Lecointre and Nelson, 1996; Arratia, 1999; Chang and Maisey, 2003; Zaragüeta Bagils, 2004; Alvarado-Ortega et al., 2008), *L. minimus* is assigned to this taxon based on the presence of a row of abdominal scutes, the fusion of haemal spines and respective centra anterior to the second preural centrum, as well as the presence of a free first hypural. Other diagnostic features of the clade, such as fusion of the second hypural with the first ural centrum are not possible to verify due to the poor preservation of the caudal endoskeleton in the new Argentinian species.

Taking into account the evidences supporting the placement of the new taxon within Ellimmichthyiformes or Clupeiformes are insufficient, it is assigned to Clupeomorpha *incertae sedis*.

We placed *vis-à-vis Leufuichthys* with some others Upper Cretaceous Clupeomorpha described in South America and Africa, in order to verify its putative affinities. Considering that there is no Clupeomorpha described to the Upper Cretaceous of Argentina (see Arratia and Cione, 1996), from where *Leufuichthys* came, we compared it with Lower Cretaceous and Tertiary forms. Additionally, we furnished a brief comparison between the new species and the well-known clupeomorphs from the Lower Cretaceous of Brazil. A more comprehensive review of clupeomorphs and certain taxa erroneously assigned to Clupeomorpha was furnished by Figueiredo (2006).

"*Haplospondylus*" *clupeoides* Cabrera, 1927 comes from the marine deposits of the Lower Cretaceous of Patagonia, southern Argentina. It was assigned to Leptolepididae (sic) by Cabrera (1927) and later recognized as an indeterminate clupeomorph by Cione (1985) mainly on the basis of abdominal scutes at the ventral midline, and also numerous epineurals, T-shaped epipleurals, and certain features of skull and scales. Due to the poor preservation of the specimen, it was also maintained as an *incertae sedis* Clupeomorpha by Cione and Pereira (1990). *Leufuichthys* shares with "*Haplospondylus*" the presence of vertebral centra fairly longer than deep, very elongate pleural ribs, short-based dorsal fin, and epipleurals in the caudal region. Otherwise, "*Haplospondylus*" shows frontal with a concave upper profile, frontal ornamented with strong ridges, and anteriormost neural spines very inclined backwards differing therefore from *Leufuichthys* (see Cabrera, 1927; Cione, 1985).

Austroclupea zuninoi Bardack, 1961 is a small fresh-water clupeid described from the Tertiary of Salta Province, northern Argentina. It is superficially similar to *Leufuichthys* in possessing a compressed and slightly deepened body, untoothed upper and lower jaws, quadrate-mandibular joint placed behind the middle of the orbit, keeled pleural ribs, and cycloid scales. Otherwise, *Austroclupea* differ clearly from *Leufuichthys* mainly by the presence of a short anal fin bearing 15–17 rays, as well as a large orbit fitting three times in head length, dorsal fin origin anterior to the pelvic fin origin, and an ornamented frontal (see Bardack, 1961; Cione et al., 1998).

Gasteroclupea branisai Signeux, 1964 was first described to the El Molino Formation, Maastrichtian of Bolivia, being also found in the Yacoraite Formation, Campanian–Maastrichtian of Argentina. It was classified in Clupeidae by Signeux (1964), being later included in the Pristigasteroidea by Grande (1985), but maintained in Clupeidae by Gayet (1992). *Gasteroclupea* is a small and very compressed fish with a prominent abdomen, showing few similarities with *Leufuichthys* such as a similar number of vertebrae (32 or 33 in *Gasteroclupea*; 31 in *Leufuichthys*), presence of elongate ribs and three uroneurals. Otherwise, it is clearly distinct from *Leufuichthys* mainly by the absence of pelvic fins and also by the presence of a short-based anal fin and preopercle with equal-sized limbs forming a slightly rounded angle between them (see Signeux, 1964; Gayet, 1992; Arratia and Cione, 1996).

In the Upper Cretaceous of Africa, particularly from Democratic Republic of Congo, there are four marine clupeomorphs: *Kwangoclupea dartevellei* (Casier, 1965), *Eoknightia caheni* (Taverne, 1976), *Nolfia kwangoensis* Taverne, 1976, and *Audenaerdia casieri* (Taverne, 1969). The latter is from the Santonian strata, whereas the first three are from the Cenomanian.

Kwangoclupea dartevellei was originally described as *Diplomystus dartevellei* by Casier (1965) and included in the Clupeidae, being however considered a Clupeomorpha *incertae sedis* by Grande (1985). It was redescribed by Taverne (1997a) as the new genus *Kwangoclupea* and suggested as a basal Clupeomorpha. *Kwangoclupea* shares with *Leufuichthys* the presence of an elongate anal fin (27–29 rays in *Kwangoclupea*; 25 in *Leufuichthys*), short-based dorsal fin, similar number of vertebrae (32 in *Kwangoclupea*; 31 in *Leufuichthys*), and a primitive caudal endoskeleton with first uroneural free from preural centrum. Otherwise, they are easily separated by the presence of a deep body with a prominent abdomen, frontal and parietal ornamented with strong longitudinal ridges, well-developed posttemporal fossa, parasphenoid garnished with a strong basipterygoid process, toothed premaxilla,

and quadrate-mandibular joint placed at the level of the anterior border of the orbit in *K. dartevellei* (see Casier, 1965; Taverne, 1976, 1997a).

Eoknightia caheni was originally considered a clupeoid by Taverne (1976), but classified as a Clupeomorpha *incertae sedis* in Grande (1985). In its redescription, Taverne (1997a) suggested it as a basal Clupeomorpha. *Eoknightia* is clearly distinct from *Leufuichthys* by the presence of quadrate-mandibular joint placed at the level of the anterior border of the orbit, pelvic fin origin placed behind the dorsal fin origin, and parhypural fused to the first preural centrum. Otherwise, they share an abdomen not hypertrophied, a pronounced prognathism, a parasphenoid untoothed and lacking basipterygoid process, and both preopercular limbs unequal in length and forming an obtuse angle between them (see Taverne, 1976, 1997a).

Nolfia kwangoensis was described by Taverne (1976) as a Clupeiodei, but suggested as a Clupeomorpha *incertae sedis* by Grande (1985), and maintained as a Clupeoidei *incertae sedis* in the redescription furnished by Taverne (1997a). The single specimen lacks head and anteriormost portion of the trunk hindering the comparison with *Leufuichthys*. It possesses a body moderately deep and abdomen without hypertrophy, similar to that verified in *Leufuichthys*. Also, both taxa show dorsal fin short-based, anal fin elongate-based, and an autogenous parhypural. On the other hand, *Nolfia* differs from *Leufuichthys* mainly by the presence of pleurostyle, and the neural spines well-developed all along the axial skeleton (see Taverne, 1976, 1997a).

Audenaerdia casieri was originally described as *Clupavus casieri* by Taverne (1969) and assigned to the Clupavidae. Later, the same author (Taverne, 1973) redescribed the fish proposing the new genus *Audenaerdia* and put it into the Clupeidae. Although Grande (1985) in his comprehensive review of Clupeomorpha have not furnished a determination to the genus, the taxonomical assignment of *Audenaerdia* in Clupeidae was maintained by Taverne (1997b). *Audenaerdia* is a small-sized clupeid fish superficially similar to *Leufuichthys* regarding the presence of untoothed jaws, small post-temporal fossa, short-based dorsal fin, six hypurals, autogenous parhypural, and three uroneurals. It can be clearly distinguished from *Leufuichthys* by the presence of a lateroparietal skull roof, small anal fin bearing 15 rays, a single epural, pleurostyle, shape of the preopercle, and complete set of epineural and epipleural intermuscular bones along the body (see Taverne, 1969, 1973, 1997b).

Gallo et al. (2006) pointed out the occurrence of a small Clupeomorpha in the Turonian of southern Brazil, representing the unique record of this taxon in the Upper Cretaceous of Brazil. It is represented by a caudal skeleton and part of the vertebral column hindering the comparison with *Leufuichthys* as it does in *Nolfia*. Notwithstanding, it is clearly distinguished from *Leufuichthys* by the presence of pleurostyle, compound centrum formed by the fusion of the first preural with the first ural centra, four to five hypurals, and the probable absence of ventral scutes. They share the presence of smooth vertebral centra, haemal spines anterior to the second preural centrum fused to their respective centra, slender parhypural, and very long caudal fin-rays.

Since the 19th century, clupeomorph fishes have been described for several basins in northeastern Brazil, especially for the Lower Cretaceous formations. The group includes a diverse assemblage composed of ellimmichthyiforms, basal clupeiforms, and advanced clupeoids (Figueiredo, 2006).

Ellimmichthys longicostatus (Cope, 1886) was described from the Neocomian of the Recôncavo Basin, State of Bahia, without a defined taxonomical position. Later, it was assigned to the Paraclupeidae into the Ellimmichthyiformes by Grande (1985), Figueiredo (2006), and Alvarado-Ortega et al. (2008). It shows a very pronounced abdominal region, dermal skull bones markedly ornamented, and short-based anal fin, features not shared with *Leufuichthys*.

Ellimma branneri (Jordan, 1910) is known in the Muribeca Formation, Aptian of the Sergipe-Alagoas Basin, State of Sergipe. It was classified within the Clupeiformes, but it lacks derived features of this group, being later assigned to the Paraclupeidae (Chang and Maisey, 2003; Alvarado-Ortega et al., 2008). *Ellimma branneri* shows a markedly convex ventral outline and a short-based anal fin (15 rays and 14–15 pterygiophores), thus differing from *Leufuichthys*.

Scutatuspinosus itapagipensis Santos and Corrêa, 1985 was described to the Neocomian of the Recôncavo Basin and assigned to the Clupeidae into the Clupeiformes, being later considered an Ellimmichthyiformes *incertae sedis* by Figueiredo (2006) and a basal Paraclupeidae by Alvarado-Ortega et al. (2008). The presence of a toothed dentary, a quadrate-mandibular joint placed at the level of the posterior region of the orbit, and a short anal fin bearing nine rays is not shared with *Leufuichthys*.

Ellimma cruzi Santos, 1990 (="*Ellimma*" *cruzae*, *q.v.*, in Figueiredo, 2006) came from the Aptian-Albian of the Pernambuco Basin, State of Pernambuco. It was allocated into the Clupeidae, being later put in the Paraclupeidae by Figueiredo (2006). It differs from *Leufuichthys* mainly by the body length (150–160 mm *versus* 46 mm in *Leufuichthys*), a remarkable abdominal convexity, quadrate-mandibular joint placed at the level of the anterior border of the orbit, and short anal fin with 12–13 rays.

Santanaclupea silvasantosi Maisey, 1993 was described from the Albian of the Araripe Basin, State of Ceará, and considered a Clupeiformes *incertae sedis*. It possesses two engrauloid conditions, an obliquely inclined suspensorium and elongate jaws, which are not present in *Leufuichthys* (see Maisey, 1993).

Codoichthys carnavalii Santos, 1994 was described to the Upper Aptian of the Grajaú Basin, State of Maranhão and put in Clupeomorpha *incertae sedis*, being later considered an Ellimmichthyiformes *incertae sedis* by Figueiredo (2006). It is a small-sized fish with a double-armored fusiform body, showing a short anal fin with 15 pterygiophores, and parhypural apparently fused to the first preural centrum, differing from *Leufuichthys*.

Ellimmichthys maceioensis Malabarba et al., 2004 is a paraclupeid fish described from the Maceió Formation, Aptian-Albian of the Sergipe-Alagoas Basin, State of Alagoas. It shows the body with an arched ventral profile and a short-based anal fin (14 pterygiophores), differing therefore from *L. minimus* (see Malabarba et al., 2004).

Pseudoellimma gallae Figueiredo, 2009 was described from the Barremian of the Sergipe-Alagoas Basin, State of Alagoas, and considered as belonging to an early lineage of Clupeiformes. It is a medium-sized fish showing frontal and parietal ornamented with parallel and longitudinal ridges, a short anal fin with 13 fin-rays, vertebral centrum ornamented with many longitudinal ridges, parhypural fused to the first preural centrum, and five hypurals, differing from *Leufuichthys* (see Figueiredo, 2009).

Other undescribed or unpublished Lower Cretaceous clupeomorphs are recorded in the Araripe and Sergipe-Alagoas basins (e.g. Maffissoni, 2000; Massa et al., 2001; Quadros and Figueiredo, 2001; Figueiredo and Gallo, 2002; Figueiredo, 2006).

To conclude, all the characters mentioned suggest that *L. minimus* differs to a greater or lesser extent from all Cretaceous Clupeomorpha described in South America and Africa, not allowing to identify it with any known taxa. Yet, the unique combination of features affords its generic status. A more detailed phylogenetic analysis of the whole group is necessary to establish if those taxa are indeed closely related.

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